

NESTING BIOLOGY OF THE SQUASH BEE
PEPONAPIS UTAHENSIS
(HYMENOPTERA; ANTHOPHORIDAE; EUCERINI)

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Abstract.—Information is presented on nest architecture, provisioning, ontogeny and certain other aspects of the natural history of the squash bee *Peponapis utahensis* (Cockerell) and compared with what is known about other species in the genus.

Resumen.—Se presenta información sobre la arquitectura de los nidos, aprovisionamiento de la celda, ontogenia y otros aspectos de la historia natural de la abeja de la flor de calabaza *Peponapis utahensis* (Cockerell). Estos datos son comparados con la información conocida para otras especies de este mismo género.

We present the following information on *P. utahensis* (Cockerell) to expand the understanding of the behavior and ecology of the bee genus *Peponapis*, all species of which are believed to pollinate squashes and gourds (*Cucurbita*). Heretofore, the nesting biologies of only *Peponapis pruinosa* (Say) (Mathewson, 1968) and *P. fervens* (Smith) (Holmberg, 1884; Michener and Lange, 1958) have been described.

OBSERVATIONS

Description of nesting site. This species visited flowers of an unidentified species of *Cucurbita* of the *sororia* group¹ and nested at Chamela, Jalisco, Mexico. We discovered the first nest entrance on October 1, 1985, but subsequent rains obliterated it before excavation. The second nest, found on October 6, was within 30 m of the first, and we encountered a third adjacent to the second one during our excavations on October 8, 1985. All nests occurred in a partly cleared, horizontal area (Fig. 1) in the woods adjacent to Arroyo Chamela, within 100 m of the closest *Cucurbita* patch. The forest canopy shaded all three entrances for most if not all of the day, and herbaceous vegetation 30 cm high also partly obscured two of the entrances. The soil was homogeneous, moist, loose, coarse sand, with little organic content except for a few roots, from the surface to a depth of about 40 cm, below which it became finer, more clay-like and compact.

Many other species of bees occurred in the area, including *Xenoglossa gabbii* (Cresson), which visited the same food plants as *Peponapis*. Considering the large

¹ *P. utahensis* has also been observed at the flowers of *Cucurbita pepo*, *Luffa* sp., *Schizocarpum longisepalum* Jeffrey (all Cucurbitaceae) and *Ipomea nil* Roth (L.) and *Ipomea* sp. (Convolvulaceae).

number of *Peponapis utahensis* foraging early in the morning, we must not have discovered the main nesting area. Although *Triepeolus*, *Epeolus*, and *Odyneropsis* were collected in the region, no parasitic bees flew around the nest entrances, and we did not recover their immatures in excavated cells.

Description of nest. Although we did not observe the opening to the third nest, the entrances of the other two were unplugged and surrounded by small concentric tumuli. Just below the surface, the main tunnel of the second nest (Fig. 2), 7.0 mm in diameter, gave rise to a short lateral (antechamber) several centimeters long, extending horizontally and ending blindly. The open main burrow meandered slightly but descended generally vertically. Whereas the burrow of the second nest was being constructed and was open its entire length, that of the third nest was filled with sand so that it was not detectable except below, where the finer substrate contrasted with the coarser sand fill. At the depth of 50 cm, the open burrow of the second nest widened and an open lateral extended outward about 5 cm and rose about 1.5 cm before bending downward and connecting to an open, partly provisioned cell. The wall of the lateral was unlined and absorbed water readily when tested. Filled laterals (Figs. 2, 3) leading to completed cells were indistinguishable from the substrate.

All cells (Fig. 4) were vertical and arranged singly. Radially symmetrical, they were elongate, 8.0–9.0 mm in maximum diameter (4 measurements) and 14.0–15.0 mm long (2 measurements from bottom of cell to rim of closure). They gradually and evenly widened from their mouths (7.0 mm in diameter) to their maximum diameters about 5 mm from the bottoms. The lower part of each cell was broadly rounded. Hence their general shape and appearance were similar to that of other eucerines familiar to us.

We encountered eight cells, all between the depths of 48 and 56 cm; some of these were associated with the third nest. Cells (Fig. 3) ranged from 5.0 to 15.0 cm from the main tunnel.

Cell walls were smooth, darker than the substrate on excavation, and not certainly plastered, although in some cases the soil immediately adjoining the lining seemed slightly denser than the substrate. (In cells of some taxa, the female seems to make a large excavation and then plasters the surface with a thick, smooth wall that, on drying, is distinct from and harder than the substrate. The actual process is not fully understood.) The lining was shiny, semitransparent, and extended from the bottom of the cell upward about 15 mm, to the level where the cell (or burrow) wall became rougher. The lining was waterproof when tested with a droplet.

Several cell closures were deeply concave spirals of coarse soil on the inside with about 5 rows to the radius. Closures did not exhibit a smooth outer surface distinct from the fill of the lateral, as is the case with certain other anthophorids such as *Exomalopsis* (Rozen, 1984).

Provisioning and development. The yellow provisions were generally mealy-moist, although they may have become quite liquid on the surface in older cells. The provisions contained air spaces (vaculated) as with many other eucerines, but the strong cheesy odor often encountered in nests of other tribal members was scarcely noticeable. The pollen grains were large and uniform in size and shape.

We did not encounter eggs, but did find small and intermediate larvae on top of the provisions, feeding around the periphery. A large intermediate larva (Fig. 4) rested on its side as it fed, and had created a central pillar of provisions.

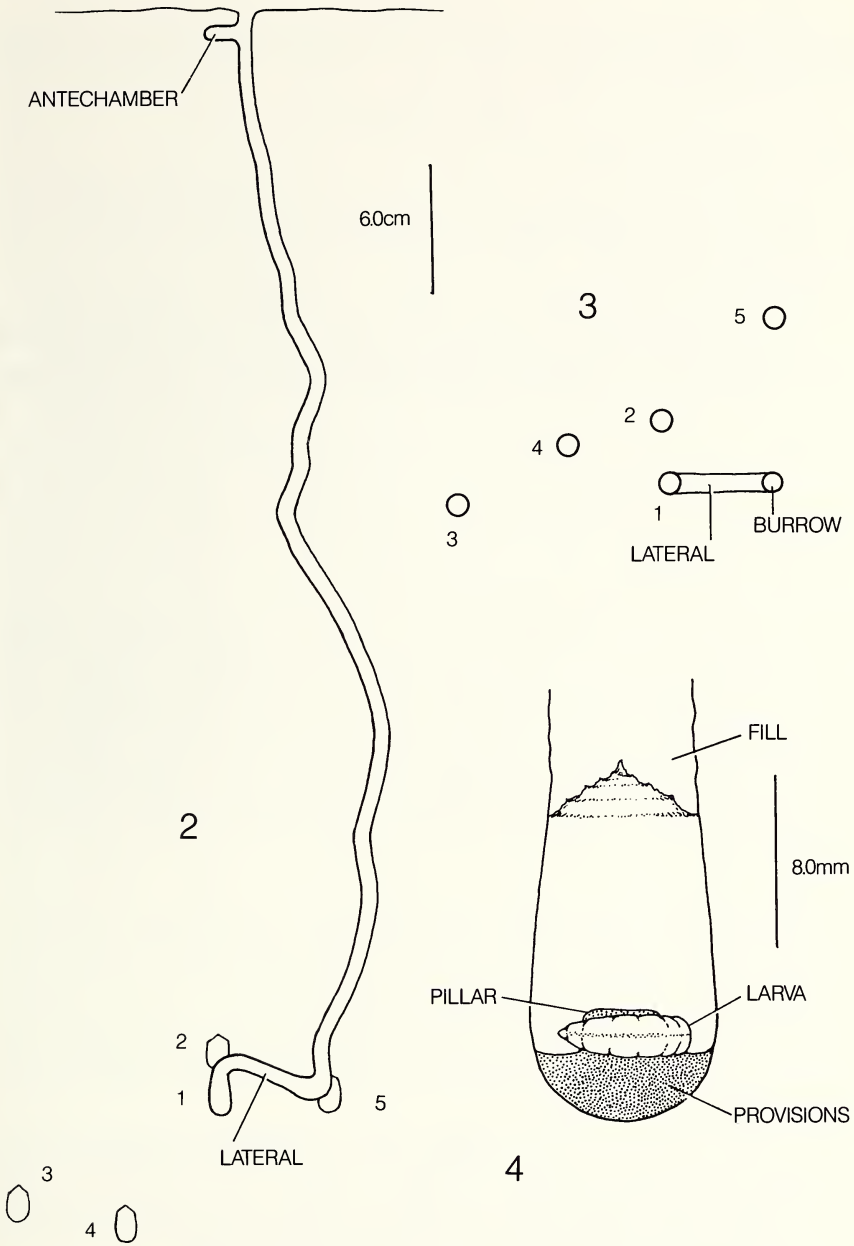


Fig. 1. Ricardo Ayala excavating nest of *Peponapis utahensis* at Chamela, Jalisco, Mexico.

A single mature larva had started to defecate by placing elongate yellow fecal pellets overhead against the cell closure, as has been seen in other eucerines. No cocoons were encountered, but the larva possessed projecting salivary lips, an anatomical feature associated with cocoon production.

Daily and seasonal activity. This species flew early in the morning. On October 1, we heard the first females on the open flowers at about 6:30 a.m. when it was still too dark to see them. Their greatest period of activity extended between 6:30 and 7:00 a.m., at which time we could observe them together with the *Xenoglossa gabbii*, a less abundant species at Chamela. Charles D. Michener (in lit.) collected "one or two in flight about 10:00 a.m., and two males in closed flowers at midday."

Peponapis utahensis as well as other species in the same genus and *Xenoglossa gabbii* were active only from September to the first days of November, coinciding with the flowering of Cucurbitaceae and Convolvulaceae in the region.



Figs. 2-4. 2. Nest of *Peponapis utahensis*, side view. 3. Same, top projection at cell level. 4. Diagram of closed cell showing closure, provisions, and feeding intermediate stage larva, side view. Scales refer to Figures 2 and 3, and 4, respectively.

DISCUSSION

We can compare the nesting biology of three species of *Peponapis*, as follows: *Peponapis (Peponapis) pruinosa* (Mathewson, 1968), *P. (Colocynthophila) fervens* (Holmberg, 1884; Michener and Lange, 1958), and *P. (Eopeponapis) utahensis* (present paper). As indicated, each species belongs to a different subgenus, as recognized by Hurd and Linsley (1970).

All three species nest in flat or nearly flat ground in the general vicinity of the pollen source, *Cucurbita*, and apparently only a single female occupies a nest. Whereas *utahensis* nests were shaded, those of *fervens* and apparently also *pruinosa* were exposed to the sun.

Burrow entrances of all species are normally surrounded by concentric tumuli, and main burrows of nests under construction are open. For *utahensis*, there is an indication that burrows of completed nests are filled. Females of both *utahensis* and *pruinosa* construct short blind horizontal tunnels (antechambers) connecting to the main tunnel just below the ground surface, but antechambers are not reported for *fervens*. The main burrow of *fervens* is described as vertical and very straight; of *pruinosa*, vertical but sometimes taking "a spiral course to circumvent buried obstacles"; for *utahensis*, meandering slightly but generally descending vertically through a homogeneous substrate. Cells of *fervens* were found 20–60 cm deep by Michener and Lange (1958) and 12 cm by Holmberg (1884); those of *pruinosa*, 12–22 cm; and those of *utahensis*, 48–56 cm. Cells occur 4–7 cm from the main burrow in *fervens*, within 12 cm in *pruinosa*, and 5–15 cm in *utahensis*. Laterals ascend somewhat before connecting to cells in *fervens* and *utahensis*, but descend in *pruinosa*. With all species, laterals are filled with soil after cell closure. Cells of all three species (and indeed of all eucerines familiar to us) are vertical and radially symmetrical. Cells of *fervens* and *utahensis* are about the same size (8–9 mm in maximum diameter, 14–16 mm long); those of *pruinosa* are slightly smaller (6.5–7 mm in diameter, 13 mm long). Although none of the species exhibited clearly plastered cell walls, those of *fervens* are reported to be harder than the substrate. Cell linings are somewhat shiny in all cases.

In all three species, the provisions are placed in the bottom of the cell. Consistency of the food at the time of deposition needs further study as do changes in consistency through time. Information on the cell closure of *pruinosa* is missing, but the closure of *fervens* is "rough on the inside and shows no spiral pattern," and that of *utahensis*, deeply concave on the inside and with a distinct spiral. We predict that further observations will reveal that all *Peponapis* have spiral, deeply concave cell closures. All three species place their feces against the inner surface of the closure, and undoubtedly all three spin cocoons.

Hence, in most respects nest architecture, cell provisioning, and ontogeny of these three species are similar. The above information suggests that there may be meaningful differences from one species to another with respect to certain features, such as choice of nest site, depth of nests, compactness of cell arrangement in a nest, cell size, inclinations of lateral tunnels, and consistency of provisions.

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